

Phodopus roborovskii. By Patricia D. Ross

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Phodopus roborovskii (Satunin, 1903)

Desert Hamster

Cricetulus roborovskii Satunin, 1903:571. Type locality "Oberlauf des Scharagol-dschin (Nan-schan) [Nan Shan, upper reaches of Sharagol-dschin River, northern Gansu, China]."

Cricetulus bedfordiae Thomas, 1908:974. Type locality "Yu-lin-fu, Shen-si [Shaanxi, China]."

Phodopus praedilectus Mori, 1930:418. Type locality "Cheng-chia-tun, Central Manchuria [Kirin Province, China]."

Phodopus roborovskii: Argyropulo, 1933:136. First use of current name combination.

Phodopus przhewalskii Vorontsov and Krjukova, 1969:102. Type locality "Peski vostoka Zaysanskoy kotlovini mezhdru Ulken-Karatolom i Akzhonom na lyevom beregu Chernogo Irtisha [sands east of Zaisan Basin between Ulken-Karatol and Akzhon on the left bank of the Black Irtish River, Kazakhstan]."

CONTEXT AND CONTENT. Order Rodentia, Suborder Sciurognathi, Family Muridae, Subfamily Cricetinae (Carleton and Musser, 1993). There are no currently recognized subspecies (Bannikov, 1960).

DIAGNOSIS. *Phodopus roborovskii* is distinguished from the Djungarian hamster, *P. campbelli*, and the striped hairy-footed hamster, *P. sungorus*, by its smaller size, cryptic sandy color of its pelage, and lack of a mid-dorsal stripe (Argyropulo, 1993; Vorontsov, 1960; Fig. 1). The braincase is rounded in dorsal view, not rectangular as in the other species, and the cusps and re-entrant folds of the upper and lower molars are directly opposite, not alternate. In contrast to *P. sungorus* and *P. campbelli*, the incisive foramina of *P. roborovskii* are ≤ 4 mm in length, and are shorter than the upper tooththrow (Argyropulo, 1933).

GENERAL CHARACTERS. The desert hamster is one of the smallest of the dwarf hamsters. The feet are "unusually short and broad, densely hairy throughout, the tubercles of both palm and sole confluent into a single blister-like mass. Skeleton of feet shortened but proportionate lengths of the bones are not specially modified" (Miller, 1910:498). The tail is shorter than the hind feet. The means and ranges of external measurements (in mm) of four Mongolian specimens are: length of head and body, 72.0 (67-76); length of tail, 8.2 (7-11); length of hind foot, 11.2 (10-12); and length of ear, 11.2 (10-12; Allen, 1940). The ranges for four specimens from Yulin are: length of head and body, 73-81; length of tail, 11-14; length of hind foot, 11.5-12; and length of ear, 12-14 (Thomas, 1908). Measurements of four specimens from Manchuria are: length of head and body, 53-60; length of tail, 7-9; length of hind foot, 10.5-11; and length of ear, 12-13 (Mori, 1930).

The fur is soft and fine, approximately 9 mm long on the back (Thomas, 1908). The dorsal color of the Nan Shan population was described as light brown with yellowish on the sides and posterior back (Satunin, 1903), that of the Shaanxi population as drab gray becoming ecru-drab to pinkish buff on the sides and posterior back (Thomas, 1908), or pinkish buff (Allen, 1940; Sowerby, 1914), and that of the Manchurian population as gray (Mori, 1930). In all cases the basal fur is slate gray, and the coat color takes on a more grayish cast during molt (Flint, 1966). The mystacial pads, mouth area, entire underparts, limbs, palmar and plantar surfaces of the feet with the exception of a naked patch at the base of the pollex, and tail, are thickly covered with pure white fur. A prominent white patch occurs above each eye and a small white patch at the base of the pinnae. The anterior half of the outer surface of the pinnae is gray to blackish-brown, the posterior half and inside, white. The junction of the dorsal and ventral pelage is well defined and sinuous, with the dorsal pelage convex upwards over the shoulders, hips, and

sides. The upper mystacial vibrissae are white, the lower black (Thomas, 1908).

The skull (Fig. 2) is delicate, with an interparietal shaped like an isosceles triangle. The rostrum is slender with narrow nasals (Allen, 1940). The infraorbital foramen is oval, resembling that of *Mesocricetus* (Satunin, 1903). The anterior margin of the narrow zygomatic plate is emarginate, but less so than that of *Mesocricetus*. The braincase is broad and deep in front, narrow and low behind. The pterygoid fossae are broad and shallow, and the incisive foramina are short and relatively broad, not extending to the tooththrow. The bullae are reduced and flattened with tube-shaped bony eustachian tubes (Argyropulo, 1933). The stapedial foramina are minute, and squamosoalisphenoid grooves and sphenofrontal foramina are absent (Carleton and Musser, 1984).

The means and ranges of cranial measurements (in mm) of 10 specimens from Shaanxi are: greatest length, 22.8 (21.5-23.8); basal length, 19.0 (17.3-19.8); palatal length, 11.1 (10.5-11.6); zygomatic width, 12.4 (11.6-13.1); mastoid width, 10.1 (9.5-11.0); width across molars, 4.5 (4.4-4.6); length of maxillary tooththrow, 3.4 (3.1-3.7); and length of mandibular tooththrow (3.1-3.7; Allen, 1940). Cranial measurements from a young male specimen from Manchuria are: greatest length, 20; basilar length, 16; condylobasal length, 18.5; zygomatic breadth, 11.5; nasals, 6.5; interorbital constriction, 3.6; breadth of braincase, 11; palatal length, 8.8; diastema, 5.7; palatal foramina, 3.2; and upper molar series, 3.3 (Mori, 1930).

Phodopus roborovskii from Mongolia, Manchuria (Heilongjiang and Jilin), and Shaanxi are smaller and of different proportions than those from Nan Shan (Thomas, 1908). The following measurements (in mm) are of the holotype, a young female: length of head and body, 90.0; length of tail, 7.0; length of ear, 14; length of skull, 24.0; basilar length, 19.0; zygomatic breadth, 14.0; cranial width across bullae, 10.8; least interorbital breadth, 4.2; nasal length, 9.0; incisive foramina length, 3.8; interparietal, 2.8 by 7.0; diastema, 7.0; length of upper tooththrow, 3.8; condylar length of mandible, 13.5; length of mandibular tooththrow, 4.0 (Satunin, 1903).

DISTRIBUTION. *Phodopus roborovskii* is found in the desert regions of the Zaysan Basin and the Tuvinskaya Autonomous Region (Tuva) in the Commonwealth of Independent States (CIS), Mongolia, Inner Mongolia, and the provinces of Xingjiang (Ma et al., 1987), Gansu, Shaanxi (Shensi), Shanxi (Shansi—Argyropulo, 1933; Corbet, 1978; Flint, 1966), Kirin, Heilongjiang (Ma, 1986; Mori, 1930), and Liaoning, China (Li, 1983; Fig. 3) at elevations



FIG. 1. Adult *Phodopus roborovskii*. Photograph taken by M. Andera (Mammal Slide Library).



FIG. 2. Dorsal, ventral, and lateral views of the cranium, and lateral and dorsal views of the mandible of a captive six month old male *Phodopus roborovskii* (Royal Ontario Museum 98595). Greatest length of skull is 24.3 mm.

of 1,200–1,450 m (Thomas, 1908; Topál, 1973). There is no fossil record.

FORM AND FUNCTION. The dental formula is $i\ 1/1, c\ 0/0, p\ 0/0, m\ 3/3$, total 16. The occlusal surface of the cheekteeth is the simplest of any hamsters. The major cusps and valleys are directly opposite, there are no pits surrounded by enamel between the cusps, and the third upper molar is extremely reduced (Miller, 1910; Thomas, 1908).

The large internal cheek pouches, extending beyond the shoulders when full, are an extension of the adoral cavity (Vorontsov, 1979) and open into the diastemal region as in other true hamsters (Cricetinae). Pouch-opening is presumably controlled by five muscles derived from the buccinatorius muscle (Ryan, 1986). The retractor muscle, a derivative of the trapezius muscle, originates from the lumbar vertebrae and inserts on the ventral and medial sides of the pouch (Ryan, 1986; Vorontsov, 1979).

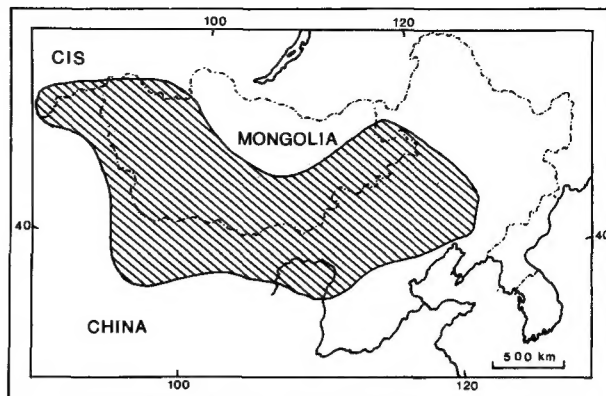


FIG. 3. Distribution of *Phodopus roborovskii* in Asia (adapted from Flint, 1966; Li, 1983; Ma, 1986; Ma et al., 1987).

The stomach consists of a corneous forestomach and a glandular stomach. In contrast to *P. campbelli* and *P. sungorus*, the corneous epithelium of the forestomach extends into the pyloric region of the glandular chamber. Pyloric glands are absent, and the number of fundic glands is restricted by the borderline fold (Vorontsov, 1979).

The small intestine comprises 60%, the large intestine 27%, and the cecum 13% of the total length of the intestine. These values are identical to those found in *P. sungorus* and similar to those of dwarf hamsters in the genus *Cricetulus* (Vorontsov, 1962).

Phodopus roborovskii, like *P. campbelli* and *P. sungorus*, has a highly effective renal mechanism for conserving water, is capable of cation concentration, but has no unique mechanisms for the excretion of excess salts. In an ambient temperature of 18°–20°C and a relative humidity of about 60%, the mean osmotic urine concentration of five males and five females captured from the vicinity of Lake Tere Khol in Tuva was 3,417 mOsm, and water secretion from the skin and lungs was 4.04 mg H₂O g⁻¹ h⁻¹. When water was withheld, urine concentration rose to 4,278 mOsm, and the loss of water through the skin and lungs decreased to 2.40 mg H₂O g⁻¹ h⁻¹ (Sokolov and Meshchersky, 1989). Under conditions of water loading (30 µl/g), *P. roborovskii* excreted less (43%) of the load within 4 hours than *P. campbelli* (70%) and *P. sungorus* (87%). Only 45% of excess potassium and sodium chloride were excreted after salt loading, just over half the amount excreted by *P. campbelli* and *P. sungorus* (Meshcherskii and Klishin, 1990).

Both genders have a mid-ventral gland that is larger in males than in females. The secretions are used for marking (Vorontsov and Gurtovoi, 1959).

ONTOGENY AND REPRODUCTION. The desert hamster breeds from April and May to September. Three to four litters are born after gestation periods of 20–22 days (Flint, 1966). Gestation periods of three consecutive laboratory-born litters, from the first post-ejaculatory lock to the birth of the first young, were 22.5, 20.5, and 19.5 days, respectively (Ross and Cameron, 1989). Based on embryo scars, the litter size is three to nine. The average litter size is six (Flint, 1966).

Neonates weigh between 1.0 and 2.1 g (Flint and Golovkin, 1961; Yudin et al., 1979). Incisors and claws are present, but the eyes, pinnae, and the digits are sealed. By day 3 the mystacial vibrissae are evident, and by day 5 gray pigment covers the back and the first dorsal hairs appear. The digits of the forefeet begin to separate on day 6, those of the hind feet on day 7. On day 8, the head is covered with hair. By day 11, the body is well-furred, superciliary vibrissae are present, and the toes are fully formed. Young are capable of hearing and the eyelids have opened by day 14 (Flint and Golovkin, 1961). Four pairs of mammae are apparent on the abdomen of females by 6 days of age, and are covered with fur by 17 days of age. Young are weaned by day 19. In contrast to *P. campbelli* young that may leave the nest as early as 2 days before eye-opening, young of *P. roborovskii* ($n = 27$) did not leave the nest until after eye-opening when locomotion was fully digitigrade (Ross and Cameron, 1989).

In 27 laboratory-reared young, the rate of increase in body mass was highest just after birth, and the growth rate of total, tail, hind foot, and ear lengths decreased gradually over the first 28 days

of life. At birth, the average mass of the young was 1.24 g, the average total length was 29.6 mm, the average length of the hind foot was 4.5 mm, and the tail was <2 mm in length. By 28 days of age, the young had attained 70% of their adult (18.1 g) mass, 100% of their adult tail length (10.2 mm), 97% of their adult (13.7 mm) hind foot length, and 95% of their adult (13.4 mm) ear length. These percentages are similar to those observed in *P. campbelli* raised under the same conditions, but the overall morphological and behavioral development of *P. roborovskii* was slower (Ross and Cameron, 1989).

Sexual activity of *P. roborovskii* in the laboratory first occurred at 4.5 months of age, 2.5 months later than observed in *P. campbelli* (Ross and Cameron, 1989). In a captive breeding colony maintained under natural conditions, *P. roborovskii* born during February did not breed until the spring of the following year when they were at least 12 months old (Hamann, 1987). Rapid aging and a high adult death rate following the breeding season led Hamann (1987) to conclude that only young animals born during the spring and summer survived the harsh winter conditions of their natural habitat.

ECOLOGY. The desert hamster inhabits areas with loose sand and sparse vegetation. It avoids solid clay substrates and areas covered with dense vegetation (Flint, 1966). Near Lake Tere Khol, *P. roborovskii* inhabits isolated barkhan dunes, 20–30 m high, which are vegetated on the leeward side with clumps of wormwood and other desert plants (Yudin et al., 1979).

Population densities are low in Mongolia (Allen, 1940) and the CIS (Flint, 1966). In the Lake Tere Khol region, *P. roborovskii* accounts for 0.7% to 4.4% of the mammals caught depending on the year and season (Yudin et al., 1979). Only three *P. roborovskii* were collected during the six (1963–1968) Kaszab expeditions to Mongolia (Topál, 1973): an adult male in a low-lying poplar stand surrounded by semi-desert (1,300 m elevation) with patches of *Haloxylon*, *Caragana*, *Ephedra*, *Zygophyllum*, and *Nitraria*; a subadult female in sand dunes over stony ground with patches of *Nitraria* and *Lasiogrostis* (elevation, 1,350 m); and a subadult male in an oasis with clumps of *Haloxylon*, *Tamariscus*, and *Nitraria* by a small stream in the Nojan Range of the southern Gobi Desert (elevation, 1,450 m). During the Central Asiatic Expeditions, only one to three specimens were trapped at each of Tsagan Nor, Shabarakh Usu, Kholobolchi Nor, and the east end of Lan Shan on the Gobi Desert (Allen, 1940).

The desert hamster is more numerous in the southern part of its range. It was reported common in the desert sandhills around Yulin, Shaanxi, and in the sand-dunes of the Ordos Desert (Sowerby, 1914).

The northern and eastern range of the desert hamster is broadly sympatric with that of *P. campbelli*, but the latter species inhabits stabilized ground such as dry mudflats, not the shifting sandy areas favored by *P. roborovskii* (Flint, 1966; Hamann, 1987; Vorontsov, 1960). In the northwestern part of its range, the desert hamster occurs with *P. campbelli* and three other hamsters, *Cricetulus barabensis*, *C. longicaudatus*, and *C. curtatus*. The diets of the species are sufficiently different to avoid competition (Flint and Golovkin, 1961).

The southwestern part of the desert hamster's range (Nan Shan and the southern Gobi) overlaps that of one other hamster, *Cricetulus longicaudatus*, and other small mammals including *Ochotona daurica*, *O. erythroris*, *O. thibetana*, *Petaurista leucogenys*, *Marmota bobac*, *Dipus sagitta*, *Meriones meridianus*, *Mus musculus*, *Microtus oeconomus*, and *Myospalax* sp. (Bannikov, 1960). In the sandy areas of the eastern steppe subregion of Meng-Xin, Liaoning Province, *P. roborovskii* is associated with *C. barabensis*, *Dipus sagitta*, *Allactaga sibirica*, and *Spermophilus daurica* (Li, 1983).

The summer diet of the desert hamster in Tuva consists almost entirely of the seeds of *Alyssum desertorum*, *Caragana* sp., *Nitraria* sp., *Dracocephalum peregrinum*, *Astragalus* sp., and *Carex* sp. (Flint and Golovkin, 1961). Although the remains of beetles, earwigs, and locusts, in some burrows of *P. roborovskii* in Mongolia indicated a diet composed almost entirely of insects (Formosov, 1929), cheek-pouch contents consisted of almost equal amounts of plant and insect material (Bannikov, 1954). Young, subadults, and adults, all store food in their burrows (Yudin et al., 1979). In Shaanxi, the desert hamster eats millet seeds, hence its Chinese name *Mi-tsang-er* (grain storer—Allen, 1940; Thomas, 1908). Captive *P. roborovskii* also eat millet, but the remains of crickets, grasshoppers, and snails, have been found in their nests (Veselovsky and Grundova, 1964).

The straight shaft of the desert hamster's burrow extends 50–150 cm into a shifting dune. The nest cavity, dug into the more solid moist sand at the end of the tunnel, contains a spherical nest constructed of shredded sheep or camel wool. The entrance is soon covered by shifting and trickling sand (Flint, 1966; Yudin et al., 1979).

BEHAVIOR. According to Sowerby (1914:69), the desert hamsters of the Ordos Desert were docile, easy to keep, and naturally tame. He wrote, "They will fill their cheekpouches to bursting point with millet or grass seed, distorting the shapes of their bodies ludicrously. Then when teased, or disturbed, they will push these pouches with their forepaws, causing the grain to pour out of their mouths. They are scrupulously clean, performing elaborate toilets at frequent intervals in their play, and being of a docile disposition attempt neither to bite nor to run away." Flint (1966), however, stated that *P. roborovskii* avoids areas of human habitation, and Hamann (1987) and Ross and Cameron (1989) reported that this species resisted taming and avoided human contact, even if handled daily from birth. In contrast to the more slowly moving *P. campbelli* and *P. sungorus*, *P. roborovskii* are lively, nimble, agile animals that move with short, jerky, almost nervous movements (Hamann, 1987).

A 16-month laboratory study of activity patterns under natural conditions revealed both daily and annual cycles. The hamsters were most active for an average of 5 h/day in November, with the peak of activity between 2100 and 2200 h. Activity dropped to <10 min/day in February and March. This was opposite the annual cycle observed in *P. campbelli*, which was active, on average, for 6.5 h/day during February and March, and only 2 h/day in November. The main daily period of activity of *P. campbelli* fell between 1800 and 1900 hours, 2 h earlier than observed in *P. roborovskii*. *P. sungorus* showed an activity profile that paralleled that of *P. roborovskii* (Hamann, 1987).

GENETICS. Karyotypes prepared from mitotic metaphase spreads and synaptonemal complexes from male meiotic cells show a diploid (2n) number of 34 chromosomes, 16 autosomal pairs, and an XY pair (Radzhabli, 1975; Spyropoulos et al., 1982). Ten autosomal pairs are metacentric, three are submetacentric, two are acrocentric, and one is telocentric (Spyropoulos et al., 1982). The X chromosome is submetacentric, the Y chromosome, acrocentric (Schmid et al., 1986). The X chromosome accounts for 6.7% of the haploid metaphase karyotype (Schmid et al., 1986) and 6.3% of the synaptonemal karyotype length (Spyropoulos et al., 1982). Synaptonemal complexes range from <10 μ m to 25.5 μ m in length (Spyropoulos et al., 1982). The fundamental number (FN), including the sex chromosomes, is 59 (Schmid et al., 1986). Spyropoulos et al. (1982) found nucleolar organizer regions (NORs) associated with the short arms of chromosomes 14 and 15, but Schmid et al. (1986) reported NORs located close to the centromeres of the long arms of chromosomes 12 and 14, respectively. The short arm of the X chromosome pairs with the long arm of the Y chromosome, and the centromeres are not aligned. At least one nuclear dense body is associated with the XY pair (Spyropoulos et al., 1982). The karyotype of the desert hamster differs from that of *P. sungorus* by seven or eight independent centric fusions, three inversions, one possible telomeric fusion, and the quantity and DNA-base pair composition of the constitutive heterochromatin (Haaf et al., 1987; Schmid et al., 1986). Mithramycin staining showed that GC-rich DNA sequences constitute the centromeric heterochromatin in the X chromosome and autosomes 9, 11, 13, and 14. These sequences are absent in *P. campbelli* and *P. sungorus*. *P. roborovskii* is believed to retain a more primitive karyotype than *P. campbelli* and *P. sungorus* (Schmid et al., 1986).

REMARKS. The holotype of *P. roborovskii*, a fluid preserved specimen, was captured in July, 1894, during the Roborovsky and Kozlov expedition to Nan Shan (Satunin, 1903). The generic name comes from *phodos*, the genitive case of the Greek *phos*, meaning a burn or blister, and *pous* (Greek), meaning foot, and refers to the large coalesced pad on the plantar surface of each foot. The species was named in honor of the collector, Lt. Roborovsky.

There is some question as to the relationship of *P. roborovskii* to *P. bedfordiae*, the form described by Thomas (1908). The nominate form is based on only a young adult specimen. Thomas (1908) believed that the two forms had different proportions and suggested that there may have been some error in the measurements given by Satunin (1903). Both forms were considered to be identical by

Argyropulo (1933), who suggested further study on the systematics of *P. roborovskii* was necessary to determine taxonomic differences among the desert hamsters. *Phodopus przewalskii* was described by Vorontsov and Krjukova (1969) on the basis of its karyotype.

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